Effects of Space and Scale in the Food Web Structure of the Aleutian Archipelago

By
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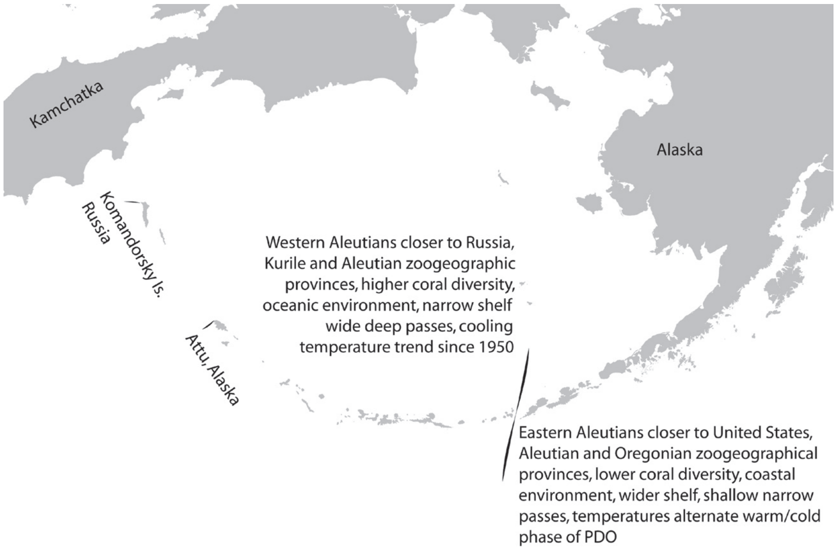


Figure 1. Marine environment and biogeography of the Aleutian Islands.

One of the challenges in fisheries management as it moves from a single-species to an ecosystem approach, is to meet the ecological and management needs of fish, seabirds, marine mammals, and humans, all of which operate over widely different spatial scales. This relatively new approach to fisheries management involves developing and fine-tuning predictive models that incorporate complex food web structures with the goal of ecosystem sustainability. A food web is a system of predator/prey relationships by which energy is passed through the parts of the system. The study of changes in the structure or function of food webs over time and space helps in our understanding of critical relationships within an ecosystem. Building successful ecosystem models requires understanding changes in the food web structure of an ecosystem depending on location. Large-scale food web models in fisheries management can adequately portray differences across ecosystems and their main features. However, large-scale food web models may not accurately represent local areas within ecosystems or those areas that comprise smaller portions of the ecosystem.

With support from the Alaska Fisheries Science Center's Resource Ecology and Ecosystems Modeling Program, we conducted a study of the effects of space and scale in the food web structure of the Aleutian Archipelago, one of the most productive fishing grounds in the nation. Our study used two ecosystem modeling approaches: 1) a large-scale food web model based on the Aleutian Islands management region, which geographically includes the central and western (U.S.) Aleutian Islands only; and 2) a series of 13 simplified standardized contiguous food web models for each 2-longitudinal degree block covering the U.S. portion of the entire eastern, central, and western Aleutian Islands.

The current management structure of the Aleutian Archipelago, as defined by the North Pacific Fishery Management Council (NPFMC), includes three regions: the Aleutian Islands (AI), Bering Sea (BS), and Gulf of Alaska (GOA). Using the large-scale food web model, we identified energy flow, predator-prey relationships, and fisheries for the Aleutian Islands management region. We then compared this model to those large-scale models for the BS and GOA and identified differences between them in basal energy pools, feeding habits, and fisheries and predation mortality. Next, using the contiguous simplified food web models we showed how the food web structure gradually changes along the archipelago, from a coastal/shelf environment in the east to a pelagic/oceanic environment towards the west. The changes in food web structure are captured primarily through the changes in prey availability, feeding habits, and local biomass of predators and fisheries removals. While the large-scale food web models provide a general pattern and framework to understand the relevance of a given species and fisheries removals, the smaller food webs capture the heterogeneity within the ecosystem and highlight more localized effects of predators and potential fisheries interactions. The smaller food web models also highlight how local effects and interactions may be masked by large-scale patterns.

Background

The marine environment of the Aleutian Archipelago has a strong boundary at Samalga Pass where oceanographic and ecological features transition from coastal to oceanic (Fig. 1). The areas east and west of Samalga Pass define two distinct environments. East of Samalga the shelf is wide, water is warmer, climate follows the pattern of the Pacific Decadal Oscillation (alternate warm and cold periods), diets are mostly neritic, and fish species from the Oregonian Province dominate. West of the pass the shelf is narrow, the water is cold and high in nutrients. Air and water temperatures have been getting colder since the 1950s, and the diversity of fish from the Oregonian Province drops significantly. Feeding habits also change and rely more on plankton and oceanic species such as myctophids and squids.

Historically, there have been five major waves of exploitation in the Aleutian Archipelago from both the east and the west: the Russian fur trade (1741-1867), American whaling (1840-1914), American colonial (1868-1940), foreign fleets (1930-1989), and modern American (1990-current) (Fig. 2). An overview of the history of exploitation in the region helps to provide an overview of the history of the ecosystem's food web. The Russian fur trade financed the discovery and exploration of the Aleutian Islands. In total, Russians exported at least 257,000 sea otter pelts and 256,800 fox furs from American territories. Fox farming was introduced relying on seabirds as feed; sea cows and spectacled cormorants were hunted for food by fur traders and went extinct. American whalers dominated the sea in the later part of the 19th century, extending their activities to the eastern and central Aleutians hunting for right whales, pelagic seals, and fish. The massive commercial exploitation of sea otters, fur seals, and whales throughout Alaska caused an increase in the subsistence hunting of Steller sea lions, which were driven to near extinction along with sea otters, walruses, and bowhead and right whales by 1910. During the American colonial period, which began when Alaska was sold to the United States (1867), there was basically no exploitation in the western Aleutian Islands. Fox farming and nearshore whaling peaked in the eastern Aleutians from 1913 to 1940. Foreign fleets came mostly from Japan and the Soviet Union, and by 1960 the fleets operated full force in the western and central Aleutians, both whaling and fishing for Pacific salmon, rockfish, walleye pollock, sablefish, Greenland turbot, Pacific cod, and Atka mackerel. Groundfish catches in 1965 reached nearly 112,000 metric tons (t).

With establishment of the Fishery Conservation and Management Act (FCMA) in 1976, foreign countries were allocated quotas based on their contribution to develop the domestic industry. These joint ventures lasted through the 1980s and shifted foreign involvement from the fleets to investments and destination markets. By 1990, fleets were domestic, with the only major port in the Aleutian Islands at Dutch Harbor in the eastern Aleutian Islands. Catches by modern American fleets remained in excess of 150,000 t throughout the decade. In 1999 the pollock fishery was severely restricted due to concerns regarding the fishery's impact on

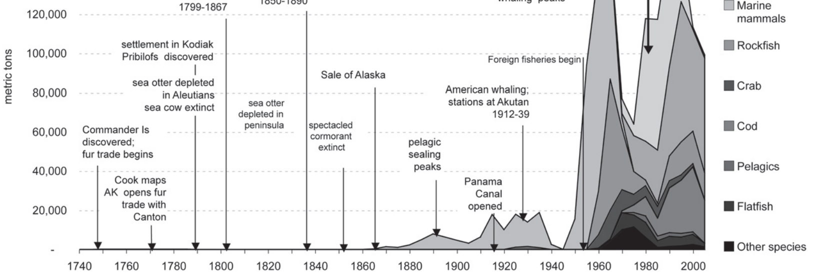


Figure 2. Timeline of historical exploitation of the Aleutian Islands with 5-year average of fisheries catches, 1745-2004.

Steller sea lions. Since then, total groundfish catches have averaged slightly above 100,000 t and are now roughly 50% Atka mackerel, 30% Pacific cod, and 15% Pacific ocean perch.

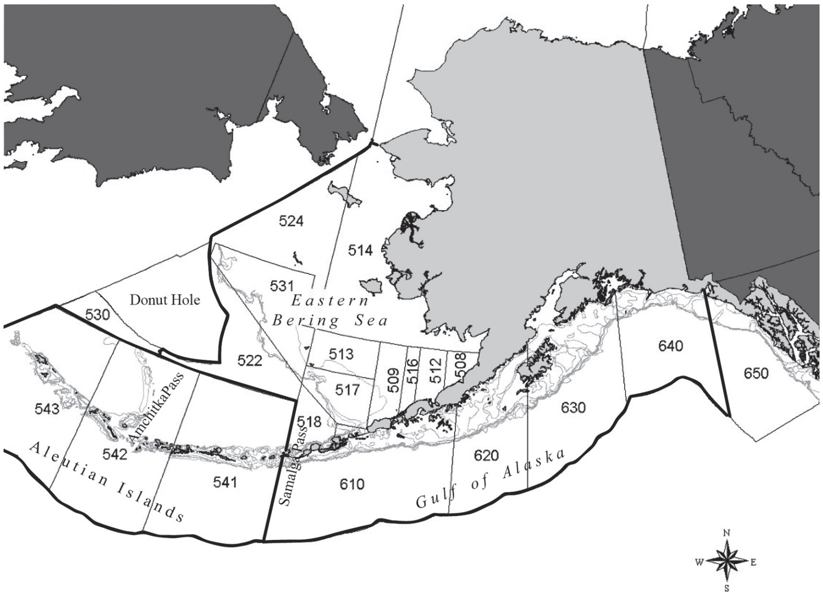


Figure 3. Current NPFMC regulatory areas: Eastern Bering Sea (EBS), Aleutian Islands (AI) and Gulf of Alaska (GOA). Numbers refer to statistical areas within regulatory areas. Note the eastern Aleutian Islands fall outside the AI regulatory area, with the northern portion falling in the EBS and southern in the GOA. Shown in gray are depth contours down to 2,000 m.

The FCMA extended U.S. jurisdiction over fisheries from 3 to 200 nautical miles and established the U.S. fishery conservation zone. This provision finally conferred to the United States authority to manage the offshore resources of the American portion of the Aleutian Archipelago, which up until then had been open for exploitation by multiple nations. The FCMA also set national standards for the use of federal marine resources and decentralized management by transferring it to regional councils which were mandated to develop fisheries management plans (FMP) compliant with the national standards. The Aleutian Islands are under the stewardship of the NPFMC and the management follows the guidelines of the Bering Sea-Aleutian Islands FMP. From the NPFMC perspective, the AI regulatory area covers the central and western Aleutians only, extending from 170°W to 170°E. The eastern Aleutian Islands fall outside the AI regulatory area, with the northern portion being of the BS regulatory area while the southern part falls within the GOA (Fig. 3).

In light of the spatial extent of the Aleutian Archipelago, its proximity to different mainlands, its wealth of resources and rich history, the historical exploitation of the region is different in the east than in the west, however it has generally been viewed on a broad scale without spatially explicit information. The lack of consistent record keeping on the historical exploitation of resources in the region prior to 1976 precludes a detailed spatial reconstruction of the regions' exploitation. With establishment of the FCMA, fishing records have served as important sources of information about the Aleutian Archipelago ecosystem, providing first-hand accounts of species present, minimum abundances, distribution, and co-occurrence. However, the emphasis on catch and abundance time series has favored a spatially aggregated view of entire ecosystems, still neglecting their heterogeneity of resources, ecology, and history, and masking the scale and local effects of fisheries and ecological processes. The use of finer spatial resolution can help identify local depletions and other changes within the ecosystem in a shorter time frame than the spatially aggregated view.

One large food web model

Our study used Ecopath to build a static mass-balanced food web model to characterize the connections between populations and fisheries within the NPFMC Aleutian Islands regulatory area. The food web model (Fig. 4) includes production and consumption estimates specific to the AI regulatory area, with biomass estimates based on surveys and stock assessments from the early 1990s. The model has substantial taxonomic detail with about 140 groups comprising benthic and pelagic fish and invertebrates, seabirds and marine mammals, and contains juvenile groups for the main groundfish species, and Steller sea lions. We present the main characteristics of the Aleutian Islands food web and highlight some of its unique aspects by comparing it to available food webs models for the EBS (eastern Bering Sea) and GOA (Gulf of Alaska) regulatory areas, built using the same methods The way in which the structure of the food webs change is best understood by looking at individual species. We take three widely distributed species that support major fisheries in the AI, EBS, and GOA— walleye pol-

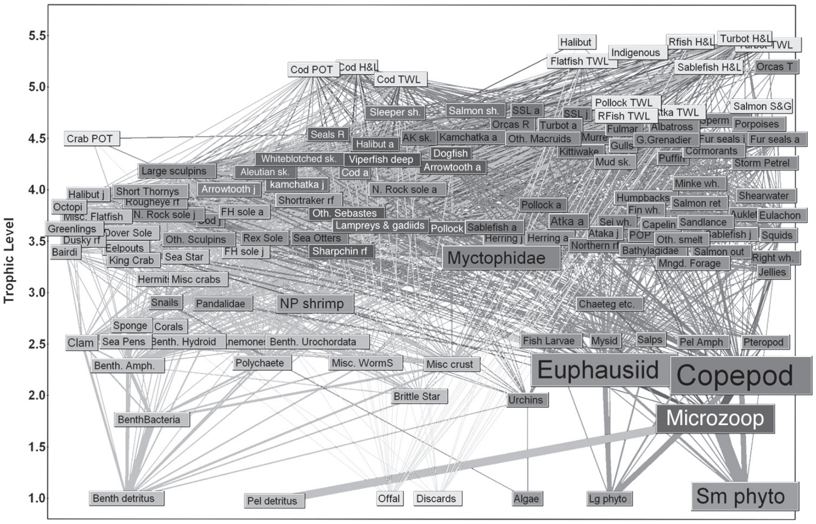


Figure 4. Visualization of the central and western Aleutian Islands food web in the early 1990s. Boxes represent functional groups, gray tones represent bottom up flow: dark for flow from primary production, medium for flow from detritus, and light for flow from fisheries. Width of lines represents strength of flow.

lock (both prey and a predator) and Pacific cod and sablefish (predators)—to showcase how the same species can play different roles across ecosystems.

Figure 5 shows a comparison of diets (prey) and sources of mortality of the three main commercial species in all three systems. Looking at the role of individual species across the three ecosystems we found that the same species had widely different roles, switching main prey items from one ecosystem to another and with different ratios of fisheries to predation mortality. Portrayed as just another component in the food web, fisheries are sometimes the only or main predator for some high trophic level species. Other times, fisheries may be a small portion of a species' mortality, having a minor role in the dynamics.

Walleye pollock feed primarily on invertebrates and plankton, but in the Aleutian Islands its main prey are fish—myctophids. Although pollock is an important prey, it is not consumed as much as in either the EBS or GOA (Fig. 5). Pacific cod prey switches from pollock in the EBS and GOA to Atka mackerel in the Aleutians, and the ratio of fisheries to predation mortality is always high (Fig. 5). Pacific cod is managed as one shared stock between the BS and AI; however, when evaluating its impact on the ecosystems, Pacific cod will have a greater effect on Atka mackerel in the AI and on pollock in the EBS, even when fished with the same intensity.

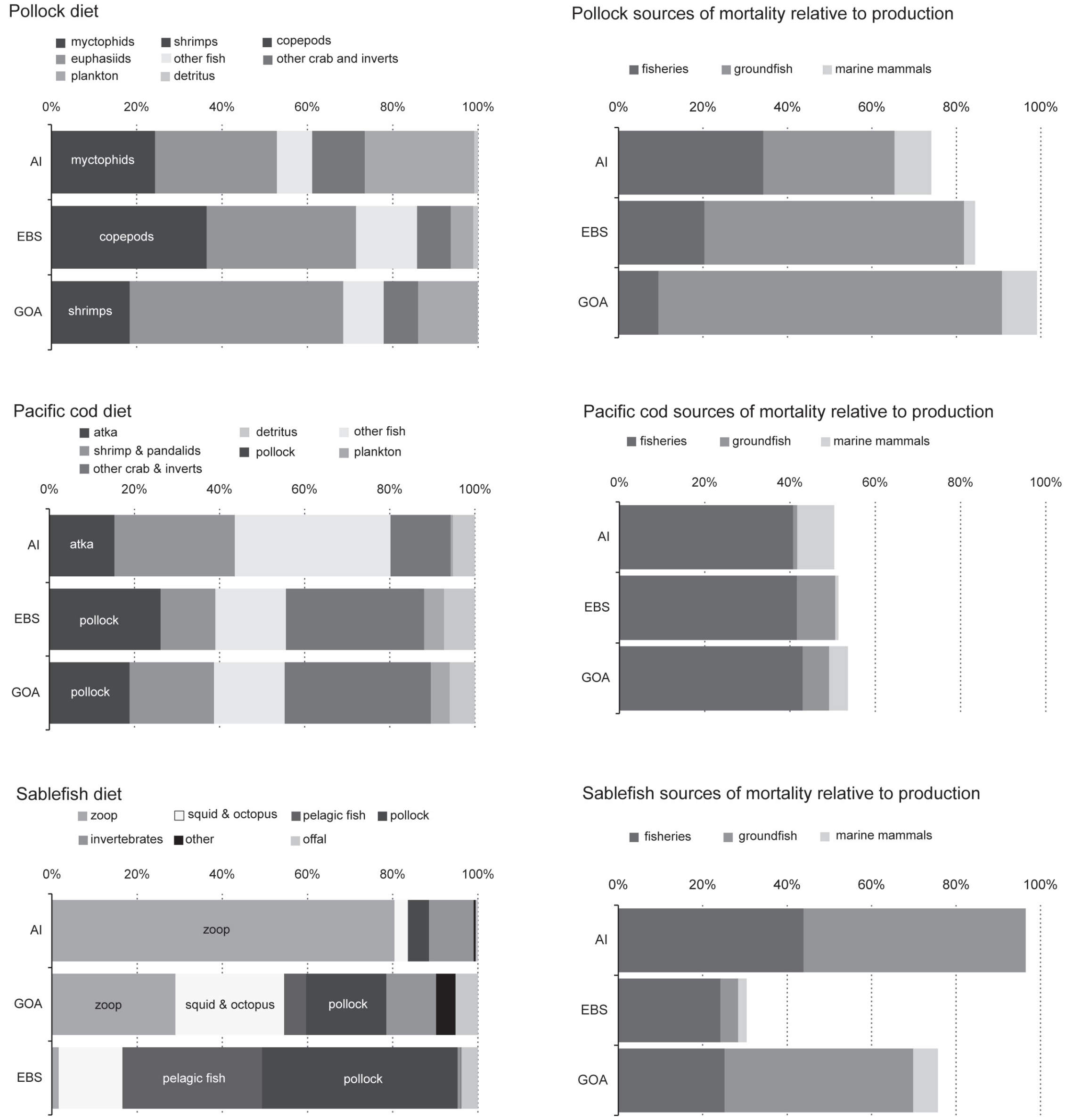
Sablefish shows one of the most drastic changes in its role in the three ecosystems. Sablefish switches from a piscivorous predator in the EBS, where its production is consumed mostly by fisheries, to a mainly piscivorous intermediate group consumed by fisheries and predators alike in the GOA, turning planktivorous in the AI. Sablefish is managed as one shared stock across the EBS, GOA and AI, but the ecosystem effects of the fishery and our ability to measure those effects across ecosystems are very different, as sablefish diet switches from commercial target species of intermediate trophic level to noncommercial species to low trophic levels. It is important to note that this pattern reflects diets of sablefish in mostly shelf rather than slope waters, so it may not be indicative of the overall adult population.

If ecosystem-based management is to be implemented successfully, a species role as either prey or predator will have to be taken into account for the long-term sustainability of species interactions. This is particularly important for shared stocks for which quotas are based on the proportion of biomass in each ecosystem only and averaged ecosystem roles may not be adequate for any one ecosystem. To tailor fisheries management to the populations interacting at different scales, different modeling approaches at various scales are warranted.

Thirteen contiguous small food webs

A joint approach of food web theory and spatial ecology should integrate food web structure across regional and local spatial scales while capturing the heterogeneity and complexity of the system. However, integrating food web structure across scales poses several challenges, with each scale having its advantages and disadvantages.

Traditional regional food web models, including those for large marine ecosystems, attempt to capture species richness and system complexity. They are often constructed based on cumulative observations over time and/or space, giving the appearance that all predator-prey links and species abundances happen uniformly in time and space. The total number of species for a large ecosystem can greatly exceed that which coexists in any fraction of that ecosystem. If all species used the same space at the same time, competition hierarchy theory alone would



Pollock diet

Pollock sources of mortality relative to production

Pacific cod diet

Pacific cod sources of mortality relative to production

Sablefish diet

Sablefish sources of mortality relative to production

Figure 5. Compared diets (left) and sources of mortalities (right) for pollock (top), Pacific cod (middle) and sablefish (bottom) across the three ecosystems: Aleutian Islands (AI), Gulf of Alaska (GOA), and eastern Bering Sea (EBS), 1990-94. Note the difference in main prey items, e.g., sablefish switches from a planktivorous diet in the AI to piscivory in the GOA and EBS. The ratio of fisheries to predation mortality is also different across ecosystems.

predict a reduced number of species coexisting by excluding inferior competitors from their preferred habitat, leaving successively restricted habitats for the lower competitors. Successively inferior competitors become increasingly aggregated over space by virtue of successive site selection processes. And so it is the partition of space (and time) that reduces the intensiy of competition, allows co-existence, and increases the number of species in a natural ecosystem.

In contrast to large-scale regional models, studies comparing habitat-specific (or local) food webs have shown that a food web's spatial location can greatly modify the identity and interactions of organisms in the web, as well as the production, storage, and movement of nutrients and detritus. Interactions among individuals and with the environment are a response to local conditions. The combined effect of spatial flows, competition, and species' range and movement pose multiple constraints on the way species are connected, resulting in unique food web structures.

So how can multiple scales be linked? Ecosystem function and biodiversity at local and regional scales can be linked if we assume community assemblages must complement each other at both levels. That is, each species falls into a particular functional role.

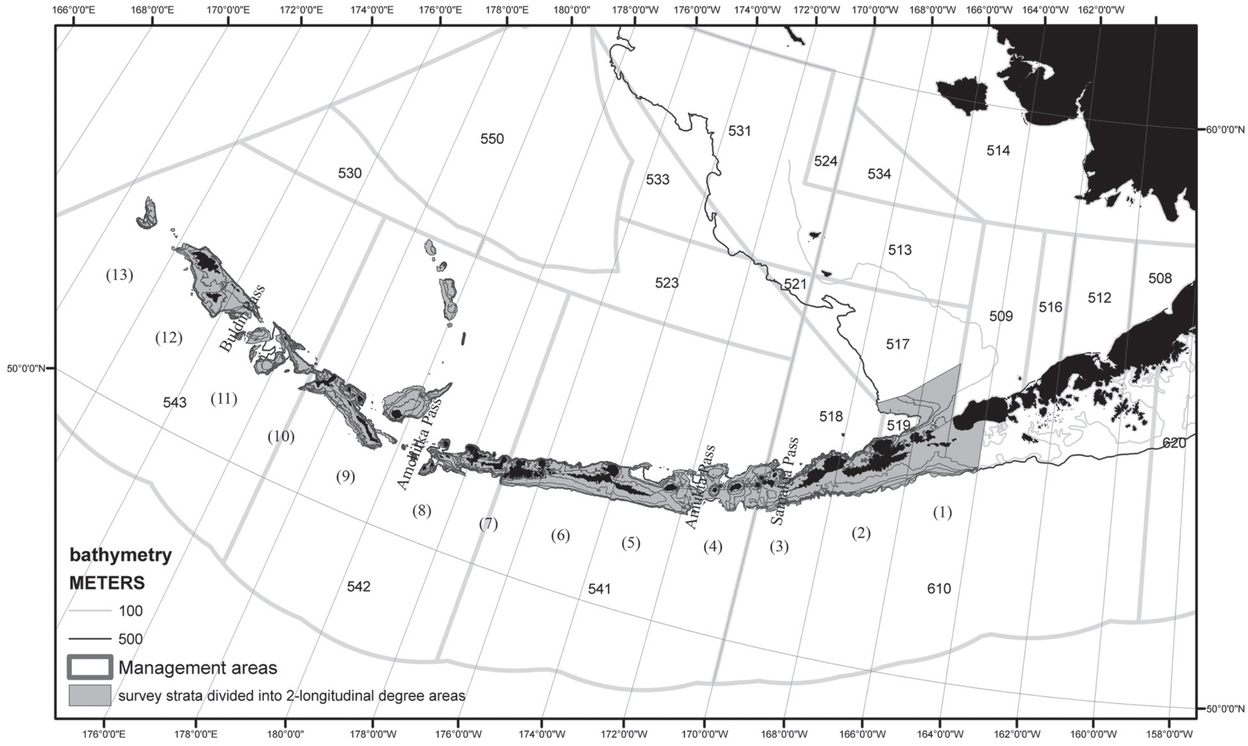


Figure 6. Area included in the longitudinal continuum model. Shaded area shows survey strata included from the Aleutian Islands and Gulf of Alaska bottom trawl surveys. Meridians show the 2-longitudinal degree divisions, number in parenthesis show the thirteen 2-degree areas for which a food web model was constructed. NPFMC management areas are shown in thick gray lines. Areas 541, 542, 543 comprise the Aleutian Islands NPFMC management region; 610 and 620 are part of the Gulf of Alaska region; the rest comprise the Bering Sea management region.

In heterogeneous landscapes some functional roles are site-specific, allowing for species to coexist in the same region but not necessarily the same site (in other words, regional coexistence without local coexistence). Site-specific and general functional roles can be filled by both permanent and temporary residents. As residents move individually and interact within their range and/or distribution, patterns arise. Looking at trophic interactions specifically, individual predators share food webs in space, and the embedded spatial structure combined with behavioral responses influence food web dynamics. This approach, like ecosystem ecology, spans across ecosystem and habitat types and spatiotemporal scales.

Presumably then, a regional food web can be split into multiple food webs of similar scale but different spatial location within the ecosystem. This construction would allow the exploration of spatial processes behind changes in food web structure—local and regional species coexistence and the spatial patterns arising from those interactions. By constructing spatial food webs from actual data, such exploration would be empirical rather than theoretical, addressing the gap between empirical and theoretical studies in spatial food web dynamics.

We increased the spatial scale and resolution of the large food web model by partitioning the entire extent of the Aleutian Archipelago, from 164°W to 170°E, into 13 contiguous 2-longitudinal degree areas and then built 13 food web models based on biomass, feeding habits, and fisheries estimates allocated among these 2-degree areas (Fig. 6). This level of spatial resolution restricted the number of groups we could include in the model as we needed area-specific parameters, particularly biomass estimates and diet composition specific to each 2-degree block. While we used biomass and fisheries estimates from the early 1990s, we had to pool data on food habits available from 1980 to 2002. We chose seven groups (plus fisheries) to comprise the 'predators' in the food web; these groups make up 60% of the vertebrate biomass in the large-scale food web model. The groups are Steller sea lions (SSL), planktivorous (6 species) and piscivorous (10 species), nesting seabirds, Atka mackerel, Pacific ocean perch, walleye pollock, and Pacific cod. These last four species are commercially important and have accounted for 85% of total catches in the AI regulatory area from 1991 to 2005. In the EBS and GOA these species make up 86% and 67% of the catch, respectively. By including these species, the models portray primary interactions between commercial and noncommercial components of the food web.

The prey items of the seven predators were grouped into the same categories as those for the large food web model. Categories contributing 10% or more to the diet of any predator in any 2-degree areas were left as individual functional groups. The rest of the prey categories were aggregated into more general functional groups. Including predators and prey, there are a total of 25 functional groups and 1 for fisheries (Fig. 7). All groups include adults and juveniles combined.

Empirical work on natural food webs shows interaction strength is skewed towards few primary prey and many secondary prey. Some studies have argued that secondary prey may be unimportant over time if they represent rare feeding interactions. This assertion was made in view of the overriding prevalence of time and space cumulative food webs with mismatched scales, where prey common over large areas mask the importance of locally relevant prey items that could influence predator population dynamics over time. Our results show the latter is the case.

Had we only considered prey that contributed more than 10% to any predator's diet over the entire archipelago, the predators modeled here would have had only between one and three primary prey items and the prey categories would have been restricted to Atka mackerel, sculpins, squids, myctophids, shrimps, copepods and euphasiids. But since we defined primary prey groups as those contributing over 10% to diet at any one of the 2-degree areas the number of primary prey increased. We identified salmon, crabs, benthic amphipods, polychaetes and gelatinous zooplankton as primary prey as well. The last three are locally relevant (>10% of total consumption) towards the west. Figure 8 compares the 13 food webs across the archipelago. The composition of the prey categories changes through the 13 food webs and highlights the importance of secondary or rare prey items which are locally relevant to sustain energy flow from lower to higher trophic levels at local scales, as exemplified by gelatinous zooplankton which is consumed the most in blocks 178°E and 180°. The switch from common to rare prey items prevents the fragmentation of food webs and potential loss of species due to 'blocked' energy passage (or lack of suitable prey). This has important implications for the management of biodiversity. At a large scale, it can identify a set of key species on which the food web largely relies on for its energy requirements. Disturbances on these species can potentially fragment the food webs by 'closing' food-web wide energy pathways. At a small scale, it can identify local pathways and emphasize the protection of locally important species.

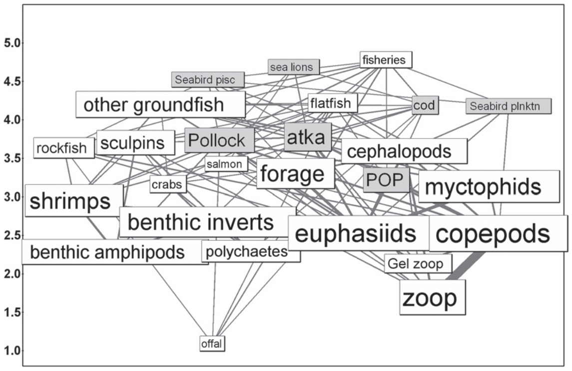


Figure 7. Basic food web constructed for each 2-degree area. The structure shown is a simplified version of the food web for the NPFMC regulatory area of the Aleutian Islands. Box size is proportional to biomass. Boxes in gray show 'predator' groups for which detailed diets/ biomass estimates were included. Diets of prey items, those in white boxes, were not included and their biomass estimates are the sum of the consumption by predators. Fisheries include removals of Atka mackerel, Pacific ocean perch, pollock, and Pacific cod. Plankton groups include euphasiids, copepods, gelatinous zooplankton and zooplankton; benthic invertebrates include polychaetes, benthic amphipods, benthic inverts, shrimp, and crab; pelagic prey includes salmon, forage fish, cephalopods, and myctophids ,and groundfish include rockfish, scuplins, flatfish, and other.

Both biogeography and the characteristics of the marine environment give coherence to the changes in food web structure across the archipelago. Three major regional food web types can be observed, one for the eastern, central and western Aleutians. While there is not a single gradient that is followed by all species, the food web characteristics in aggregate do show the food webs transition from primarily coastal/piscivorous character in the east to primarily oceanic/non piscivorous in the west (Fig. 8). With this, we now have three different levels of resolution in the food web structure across the Aleutian Islands (2-degree areas, regional and ecosystem-wide) (Figs. 8 and 4).

The 13 contiguous food webs developed in our study serve as replicates to explore how predators adjust to changes in food web structure across space. Because the populations of these predators are distributed over larger spatial areas than those covered by any individual 2-degree food web model, the food webs are spatially correlated. Neighboring food webs may represent alternative states with different dominant species that do not completely exclude their competitors. These different food

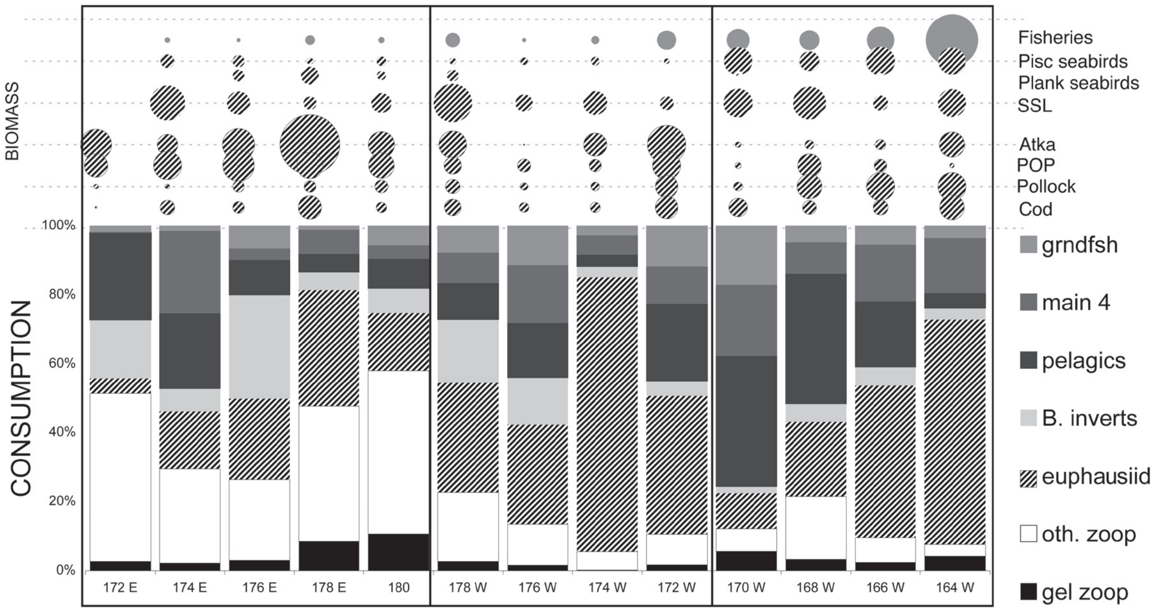


Figure 8. Compared trophic structure across the 13 food webs in the Aleutian Archipelago (early 1990s). Each vertical series represents the food web for that 2-degree area. Circles are proportional to predator biomass in tons. Steller sea lions (SSL) and seabirds were scaled 150 times larger so they would show. Biomass of consumed prey (column graph) represents the total biomass consumed per year by predators (Atka mackerel, Pacific ocean perch (POP), cod, pollock, seabirds, and SSL). Fisheries removals include those of (Atka mackerel, POP, cod and pollock). The rectangles in bold group three major types of food webs, from left to right: western, central and eastern Aleutians showing the shift from primarily nonpiscivorous food webs (western) to mostly piscivorous ones (eastern). Note prey composition within each prey category changes along food webs but this level of detail is not shown in the graph. Gelatinous zooplankton is shown to exemplify a prey item of localized relevance (in blocks 178°E and 180°).

web structures may facilitate regional coexistence. The variation within the three general food web structures hints at feasible directions in which the system may respond to changes in species abundance and composition.

Fisheries removals can move the structure of food webs along a range of states by modifying the degree to which species coexist. This proportion refers not only to total abundance but to density, which affects density-dependent interactions. The effects of fisheries are cumulative with those from environmental sources and local population dynamics. So individual impacts, although small, can have a greater effect when added to the other impacts. The natural variability in populations and environmental conditions can not be controlled, but the magnitude, frequency, and location of removals can. Understanding the range and correlations of food web structures existing within an ecosystem may inform management of the impacts of fisheries removals. The challenge for ecosystem-based management is to find a way in which to minimize and mitigate these impacts while maintaining economically sustainable fisheries.

What information from local food web models can be useful for management? One application is to compare the amount of mortality caused by fisheries to the amount caused by predation (Fig. 9, top). An improved spatial distribution of the catch would aid in lowering the risk of localized concentrations of removals, as well as the competition between fisheries and predators for local production. A ratio of fisheries-to-predation removals of 1 or higher implies a stronger interaction among them than in areas where the ratio is below 1. In other words, the more fisheries remove prey from the system the more they compete with the system predators.

Another application of the local food web model is to compare the amount of production by prey to the amount of removals by fisheries and predation (Fig. 9, bottom). For example, even when the production at the stock or ecosystem level can support both fisheries and predation removals there could be specific areas (or periods) where production is not enough causing some local or temporary depletion.

Current management of the fisheries is based mostly on estimated total allowable catches (TAC), which have no spatial components, and the assump-

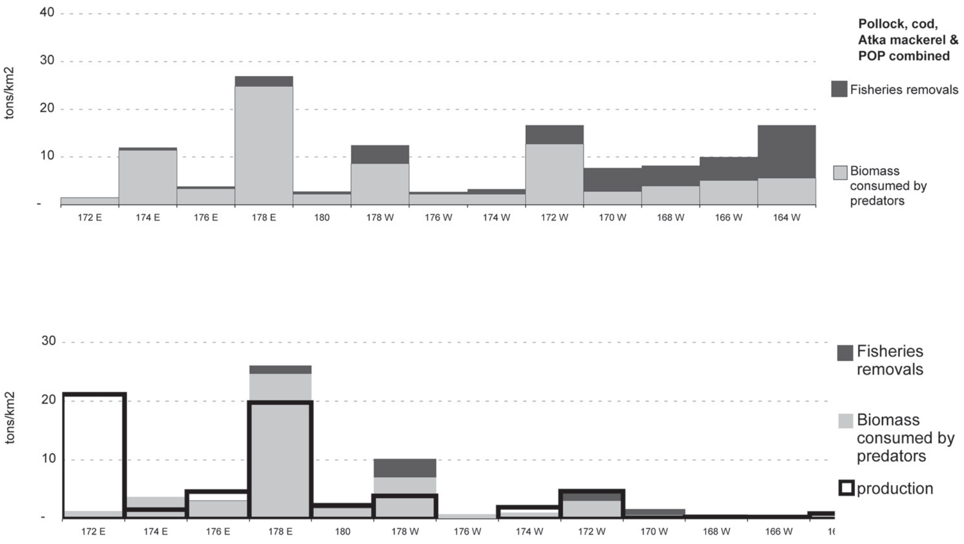


Figure 9. Applications of local food webs. Top (Application I): Fisheries vs. predation for the years 1990-94. Density of removals by fisheries and predation of pollock, cod, Atka mackerel and Pacific ocean perch (POP) combined shown by 2-degree areas. The ratio of fisheries vs. predation shows areas where competition may be higher. Bottom (Application II): Production compared to removals by fisheries and predation of Atka mackerel, 1990-94. Even though total stock production may be enough to satisfy total removals by fisheries and predation, this may not be the case throughout the ecosystem. Here, we show how local production in some areas may fall short of satisfying both fisheries and predation removals. Areas 172°E to 170°W fall within the Aleutian Islands NPFMC regulatory areas. Areas 168°W to 164°W fall within the EBS and GOA NPFMC regulatory areas.

tion of a stock-wide spatial scale as sufficient underlies most single-species assessment models. Spatial considerations and multiple scales do not necessarily have to be incorporated directly into the assessment models. Some studies have found that the production estimates from spatially explicit models do not differ in general from those based on nonspatial assumptions. If so, then multiscale spatial considerations may be implemented in the allocation of the TAC, not the assessment models. The spatial variation in the density of removals and production shows the TAC could sometimes be distributed better by incorporating the distribution of biomass and/or production. This would prevent the localized concentration of removals over small areas. The estimates for this study are based on the early 1990s, and some steps have been taken in this direction since then. For example, the TAC for Atka mackerel and Pacific ocean perch for the AI management are routinely divided among its three statistical areas based on biomass distribution stemming from the trawl surveys. Unfortunately, TAC allocation among the three statistical areas is not necessarily applied to bycatch species or all targets species in the Aleutian Islands (e.g., sharks and skates). Diffusing the removals lowers the risk of spatially concentrated removals and potential localized depletions.

Conclusion

Large-scale food web models are becoming mainstream and adequately portray differences across ecosystems and their main features. However, they may not accurately represent local areas of ecosystems or those areas that comprise smaller portions of the ecosystem. Because species and processes occur over different spatial scales, food webs inherently operate as multiscale spatial processes. We find that different scales inform each other, with larger scales and food webs providing a basic framework and key overall species while smaller scales provide feedback on more local conditions. Because fishing fleets operate unevenly and usually at smaller scales, multiple scales are needed to bridge between regional management goals and smaller-scale management tactics, such as area closures and quota allocation. The use of multiple scales and modeling approaches can help managers set ecosystem-wide goals while tracking changes and tailoring tactics to match the smaller-scale human-environmental interactions, supporting the long-term spatial integrity, continuity, and economic viability within and across ecosystems.